

THE ANNALS
AND
MAGAZINE OF NATURAL HISTORY.

[SECOND SERIES.]

No. 59. NOVEMBER 1852.

XXX.—*On a new Genus of the Family of Volvocineæ.*
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[With a Plate.]

THE number of imperfectly known organisms in the animal and vegetable kingdoms is already so considerable, that to increase it might, under ordinary circumstances, be regarded rather as burdening than enriching science; this, however, is not the case in respect to forms which not only come to fill up a vacancy in systematic arrangement, but contribute, in the phenomena of their morphology and development, new material for the solution of more important and general questions. On these grounds I believe that the form which is now, so far as I know for the first time, fully described and figured, deserves the attention as well of botanists as of zoologists, both of whom will claim it as their own especial property.

I owe my first acquaintance with the elegant organism constituting the subject of this essay to my friend Dr. von Frantzius. During a journey through Tyrol in the year 1850, he observed at Salzburg a green mucilaginous colouring of rain-water which had collected in the hollow of a grave-stone in the churchyard of St. Peter; the colour was caused by the presence of innumerable colourless vesicles, moving about like Infusoria, containing eight small green globules arranged at regular distances at their periphery. They were accompanied by *Chlamydococcus pluvialis*, which is common in such hollows in stones. The first discoverer was M. Zambra, an optician of Salzburg, who was, as I am informed by Dr. Frantzius, the delineator of the figures in Werneck's

* Translated from Siebold and Kölliker's *Zeitschrift für wissenschaftliche Zoologie*, vol. iv. p. 77, 1852, by A. Henfrey, F.R.S., F.L.S.

celebrated illustrations of the Infusoria; this gentleman had regarded the moving globules as a new Infusorium, which he called the *wreath-animalcule*; Dr. Frantzius, on the other hand, looked upon it as a *microscopic Alga* which must form the foundation of a new genus (see Frantzius's *Naturhistorische Reiseskizzen aus dem Salzkammergut und Tyrol*, Siebold and Kölliker's *Zeitschrift f. wiss. Zoologie*, iii. part 3).

So much the pleasanter was my surprise in finding a large quantity of the elegant *wreath-animalcules* in a living condition, a few days after I received the above information. I had taken advantage of the Whitsuntide holidays of the past year (1851) to explore our Silesian highlands, and used that opportunity of seeking out the granite block, almost classic in the history of microscopic organisms, on which our first German lichenologist, Major von Flotow of Hirschberg, discovered his *Hematococcus pluvialis*, ten years ago. Through the friendly instructions of this distinguished naturalist I soon succeeded in finding the stone, which forms a bridge across a ditch in the neighbourhood of Hirschberg: lying in the path between the village of Grunau and its church, this stone has in the course of time been so worn away by the number of church-goers, that it now presents a large irregular hollow; in this the rain-water collects, which, like the stone itself, is inhabited by millions of *Chlamydococcus*-globules. When, however, I collected water from this place myself on the 17th of June, to my amazement I found, scattered individuals of the *Chlamydococcus pluvialis* indeed, but a far greater quantity of the inseparable companion of the *Chlamydococcus*, the beautiful rose-red Rotifer *Philodina roseola*, which always occurs with the red *Chlamydococcus*-globules in Silesia, at Liège and Giessen, in the lake of Neufchatel, and even in the eternal snow; and moreover I at the same time detected in the water numerous specimens of that elegant wreath-animalcule with which I had already made acquaintance from the sketches of Dr. von Frantzius. Major von Flotow informed me, at the same time, that he had seen this remarkable form as long ago as the end of June in the year 1846, and had applied to Ehrenberg respecting it, but had not received any answer from him. I brought home to Breslau a bottle of rain-water from this granite block, for the purpose of further investigation, and this furnished me abundant material for the following researches.

I. Organization.

The organisms I am now about to describe exhibit an extraordinary variety of size and shape, but they are all essentially of similar structure, and consist, as already mentioned, of *eight green spherical corpuscles having their central points situated at the cir-*

circumference of a circle (Pl. VI. fig. 3 b, b), and of a large common envelope, enclosing the former as a colourless vesicle, at the equator of which are ranged the said eight green globes (fig. 3 a).

The common envelope is bounded by a membrane wholly devoid of structure and transparent, so that it may be overlooked if the illumination be not properly modified, under which circumstances the eight green globes appear destitute of any common bond of union. But the *membrane* of the envelope always exists, and although very delicate and thin while young, it becomes thickened with age, and then possesses an evident breadth, albeit no compound structure can be detected. *The membrane of the envelope is absolutely rigid* and never changes its shape, excepting through the ordinary expansion of growth; therefore it is not only totally devoid of contractility, but is even elastic only in a slight degree.

In whatever direction the total organism may lie during its movements, the envelope always appears as a perfect, absolutely regular circle (figs. 1, 2); thence it results most decidedly that the *membrane of the envelope forms a sphere*, which may perhaps deviate but very little from the mathematical ideal. The diameter of the envelope varies between tolerably wide limits; while younger forms possess an envelope some $\frac{1}{80}$ th of a line (0.028 mm.) in diameter, most attain one of $\frac{1}{30}$ th (0.044 mm.); and the largest are as much as $\frac{1}{40}$ th of a line (0.055) in diameter.

The phenomena in dissolution and during propagation prove that the membrane of the envelope immediately surrounds a colourless watery fluid, the refractive power of which does not differ from that of water. The envelope may therefore be regarded as a broad, spherical *cell* with a delicate structureless membrane, colourless and transparent like glass, containing a thin, water-like, colourless fluid; consequently I shall denominate it the *envelope-cell* (*Hüll-zelle*).

While the envelope-cell varies generally speaking only in size, and no difference whatever of shape and structure can be detected in the different individuals, the variations in the development of the *eight green globes* in its interior are very great (fig. 3 b, b). In fact it is difficult to represent the multiplicity of forms which here display themselves, so as to give a full and clear idea of them; and our figures even can afford but a very insufficient picture, since scarcely a single individual exactly resembles another, in this respect. The eight green bodies in the interior of each envelope-cell, which, for reasons to be given hereafter, I shall call *primordial-cells*, are in their simplest condition globular, and stand at equal distances in a circle at the largest circumference of the envelope-cell, so that the whole

structure looks like a hollow glass globe with a ring formed of eight green globules in its interior (figs. 1, 3). If the circular line in which the centres of the eight primordial-cells stand, is regarded as the *equator of the envelope-cell*, we ordinarily find their position such that the equatorial zone lies parallel with the plane of the object-glass, and the observer consequently looks down upon the pole of the envelope-cell (figs. 1, 3, 14). In this, the *polar view*, the eight primordial-cells stand in a perfect circle and are placed very close to the circumference of the envelope-cell. The distances between the primordial-cells are more or less considerable according as they are proportionately larger or smaller; sometimes they constitute an elegant wreath composed of eight large green rosettes, almost without any intervals between them, or resemble an interrupted eight-angled star (figs. 1, 14); sometimes the green globules are so far apart as to look like the eight spokes of a wheel (fig. 3). The diameter of a primordial-cell in the polar view amounts, in the former case to $\frac{1}{120}$ th of a line (0.012 mm.), in the latter to $\frac{1}{330}$ th (0.0065), —on an average to $\frac{1}{250}$ th of a line (0.0087 mm.).

When, however, the whole revolves, so that the axis passing through the two poles of the envelope-cell lies parallel with the stage of the microscope, and the equatorial zone marked by the eight green primordial-cells stands perpendicular to the latter, consequently in the optic axis of the microscope, the envelope-cell still looks like a circle, because it is a sphere; but the eight primordial-cells, lying in one plane, are then projected in a line which corresponds to the diameter of this circle, so that the whole resembles, under the microscope, a colourless disk cut in half by a green zone (figs. 2, 4, 5). And in this, the *equatorial view*, according to the position, the four primordial-cells in the anterior hemisphere sometimes completely cover the four behind, so that only four are seen altogether; sometimes the latter appear through the interspaces between the former, and all eight are seen in one line. This view also of course gives very different pictures according to the size of the primordial-cells and the distance between them (Pl. VI. figs. 2 & 4).

Between the polar and equatorial views lie countless intermediate positions in which the ring of primordial-cells, more or less contracted, appears as an ellipse, with its longest axis constantly in the diameter of the envelope-cell, while the shorter axis appears longer or shorter, and the separate primordial-cells are approached more or less towards each other according to the laws of projection (figs. 9 & 10).

Besides this difference of the aspect which one and the same individual affords merely in consequence of the different *positions* resulting from its movements, a still greater variation is displayed

in the *shape of the green primordial-cells themselves*. I have called them globes above; properly they are always acuminate to some extent, in the form of a pear, toward the periphery of the envelope-cell, and they are imperceptibly attenuated to a point here, from which *two cilia* pass out (fig. 1). *These cilia therefore arise from the primordial-cells inside the envelope-cell*, and they emerge freely into the water through minute orifices in the latter: from the analogy with *Chlamydococcus*, I conjecture that there is a separate passage for each cilium, so that the orifices corresponding in each case to the primordial-cells are placed in pairs, and all sixteen orifices occur in the equator of the *envelope-cell*. Hence in the polar view the eight pairs of cilia go out from the circumference of the envelope-cell like elongated rays (Pl. VI. figs. 1, 3, 14).

The primordial-cells moreover *expand principally in the direction of the axis perpendicular to the equatorial plane*, so that in the equatorial view they appear, not spherical, but rather elliptical, or even sometimes stretched so considerably in this direction, that they become cylindrical or almost spindle-shaped, without undergoing any remarkable enlargement on the other axes (fig. 4 corresponding to fig. 3). If in this case the primordial-cells are large and near together, they form in the equatorial view a broad green zone inside the colourless envelope-cell, filling up a more or less considerable portion of this (fig. 2), while in the polar view they form only a circular wreath. In some instances the proper green body of the primordial-cells is only shortly cylindrical; but it becomes elongated at both ends into long beaks which reach almost to the poles, and give each primordial-cell something of the shape of the *Closterium setaceum* figured by Ehrenberg (Infusionsth. vi. 9). In this case the whole resembles a sphere surrounded by eight green bands placed in meridians and swollen only in the equatorial region. But even in this very frequently occurring, preponderating development of the one dimension, the cilia of each primordial-cell are sent out from the middle of its shorter axis, and when the primordial-cells appear projected in a zone, in the equatorial view, the motile cilia are visible only at four points of the diameter (Pl. VI. fig. 4).

The primordial-cells are very frequently developed unequally in the two hemispheres of the envelope-cell; they are not then divided into two equal halves by the equator of the envelope-cell, but show themselves crowded principally into one hemisphere, which they almost fill, and they reach almost to the pole there, while they occupy but a far smaller portion of the other, which consequently appears in greater part colourless (fig. 5). In such a case the primordial-cells almost touch with one end, while

they diverge widely at the other, and thus they look like a kind of basket composed of eight pieces, like the gaping dental apparatus of a Chilodon.

Besides the two cilia which pass out from each primordial-cell, through the orifices of the envelope-cell into the water, the former very frequently send out other prolongations, which however do not perforate the envelope-cell. These are *colourless mucilaginous filaments, going out from each primordial-cell, especially from the ends of their longer axes*, and which hence present themselves especially clearly in the equatorial view. The ends of the primordial-cells are mostly not green but colourless, and elongated into numerous, likewise colourless, broader or thinner bristle-like processes, which run out like rays in all directions, are often ramified, and are attached to the inside of the envelope-cell, without however perforating it (figs. 2, 4, 5). If these filaments are much developed, they form a proper network, which maintains each primordial-cell floating in the common envelope. The extremities of the primordial-cells are also frequently divided dichotomously into colourless mucilaginous bands, which again branch into radiating filaments and thus produce the most wonderful forms. These colourless, filiform prolongations of the primordial-cells may also be seen in the polar view, stretching in all directions, and giving the total structure a most strange aspect, almost similar to that of a Xanthidium (Pl. VI. figs. 6, 7).

In the *internal organization of the primordial-cells*, all that can be made out is a green-coloured, softish substance of which they are composed, and in which numerous delicate granules or points are imbedded. When the primordial-cells are actively vegetating, they are of a transparent vivid green; but the colour exhibits various tints; in the youngest conditions it is purer, more yellowish green, less obscured by dark points; in the largest forms, on the contrary, the contents appear brownish green and opaque, with the dark granules multiplied to such an extent, that the whole almost loses its transparency. In the middle of the primordial-cells are found *two larger, nucleus-like vesicles*, mostly symmetrically placed, and these examined separately appear annular, so that they possess an internal cavity; iodine colours them remarkably dark, with a violet tinge (figs. 2, 3, 4, 5). The centre of each primordial-cell is frequently occupied by a lighter circular space, which however does not vanish periodically, and therefore cannot be regarded as a contractile vesicle.

The primordial-cells are not surrounded by any special rigid membrane; and this is not only made evident by the multifold changes of form which they undergo in the course of vegetation, and by the filiform prolongations and ramifications which are produced directly from their substance, but is clearly shown by

the transformations which the primordial-cells pass through in consequence of external influences. Under certain circumstances, namely, the filiform processes may be retracted, being torn away from the envelope-cell and taken up into the substance of the primordial-cells; the produced ends of the primordial-cells also disappear, the latter becoming rounded off into their original spherical or short cylindrical form. Such a change would be impossible if the primordial-cells were surrounded by a rigid membrane, such as that of the *envelope-cell* for example. Still more rapid and decided are the metamorphoses which the primordial-cells undergo in the interior of the envelope-cell, through influences destructive to the life of the organism. These phenomena, usually called *dissolution*, do not change the rigid envelope-cell at all; but they totally decompose the primordial-cells, depriving them of their form and dissolving them into a single structureless green mass, which lies upon the inside of the envelope-cell, frequently destroying all evidence of the origin from eight spheres, while not a trace of special enveloping membranes comes to light. These phenomena of dissolution moreover indicate that the envelope-cell, as I have already mentioned, is composed of a delicate membrane enclosing a clear watery fluid, which cannot be dense, gelatinous or mucilaginous, since it is readily displaced by the radiating filaments and the dissolved substance, and which therefore is very similar to pure water, if not exactly the same.

II. Motion.

The *cilia* which are protruded from the equator of the envelope-cell are but short inside this, but the portion projecting into the water is much longer and vibrates actively, thereby causing all the movements. During their vibration the cilia are difficult to detect; but when dried on glass, and still better by wetting them with iodine, they may readily be traced in their whole length, especially if sulphuric acid is added, this rendering them more distinct and giving them a darker colour. The motion of the entire organism, depending on the eight pairs of cilia, exactly resembles that well known in the *Algae and many Infusoria*. First there is a rapid revolution round that axis of the envelope-cell which passes through its poles and stands perpendicular to the ring of primordial-cells, so that the envelope-cell rotates like a wheel upon its axle. In the polar view (figs. 1, 3) our form gives exactly the impression of a revolving wheel, while in the equatorial view (figs. 2, 4), where the primordial-cells are mostly elongated, it has more the aspect of a globe turning upon its axis. Besides this revolution on its axis, which endures throughout the whole life, there is an advancing movement, which pro-

duces a very irregular course; in this way these organisms screw themselves, as it were, onwards in the water. Sometimes they swim straight out with uniform rapidity, the pole going first, the rotating ring of primordial-cells standing at right angles to the course and appearing only in one line; sometimes they turn round, so that the equatorial plane presents itself as a circle again (in the polar view): they rotate thus round their centre without moving from the spot; then they set one pole forward and swim on in another direction, bend to the right or to the left, or turn quite round, mostly without any perceptible obstruction, move in curves of the most varied kinds, run round any point in spiral lines, come into different planes, sometimes ascending, sometimes descending; in short, they exhibit all those most complex and wonderful phænomena of locomotion, which we are acquainted with in the moving propagative cells of the Algæ, and, as I have demonstrated elsewhere*, in *exactly the same way* in the *Astomous* and *Anenterous Infusoria* (*Monadina*, *Astasiaæ*, *Cryptomonadina*, &c.), and which certainly do not bear at all the character of purposing, conscious volition, but appear as an activity determined not indeed by purely external causes, but by *internal* causes in the organization and vital process. The collective idea of such motions is best represented by the course described by a top which runs through the most varied curves while at the same time constantly revolving on its axis.

I have endeavoured in vain to determine whether the rotation round the axis, in the organism here described, is constant in one given direction. To render such a determination possible, it would first of all be requisite that the rotating globes should allow the recognition of a right or left, or what is the same, a top and bottom, and the marking of these by morphological differences. Such a determination, however, is altogether impossible in very many cases, in our organisms, since the envelope-cell, as we have seen, is a perfect globe, while the primordial-cells are mostly symmetrically developed toward each end in the longer axis. Under such circumstances there exist no characters for the distinction of the two poles of the envelope-cell, to regard one as the upper, the other as the lower; and in the same cases to demonstrate a revolution in one fixed direction is altogether out of the question.

We might certainly distinguish the two poles by calling that the *upper* which goes first in the motion. In many cases such a difference is already given in the organization, where, namely, the primordial-cells are unsymmetrically developed, projecting

* Nachträge zur Naturgeschichte des *Protococcus* (*Chlamydococcus*) *pluvialis* (Nova Acta Ac. C. C. L. n. c. xxii. pars 2. p. 735).

chiefly into one hemisphere of the envelope-cell. In this way we possess at least the *possibility* of making out whether the revolution takes place to the right or to the left. But in both cases it is found that the rotation of the envelope-cell is not at all constant in *one* direction; for not only do different spheres revolve some to the right and others to the left, but even one and the same individual rotates for a time with striking rapidity towards the right, the rapidity gradually slackens, the globe rests for a moment, and the moment after it revolves towards the left, with gradually increasing rapidity, and after some time the rotation returns again in a similar manner to its revolution toward the right. Although, therefore, Alex. Braun describes a *constant* revolution to the left in the in many respects analogous swarming-cells of *Chlamydococcus* and the swarming-spores of *Cedogonium*, and to the right in the moving gonidia of *Vaucheria* and the families of *Pandorina**, I must assert, *that no such constant law of revolution exists in the structure here described*†.

III. Systematic Position.

In the foregoing pages I have confined myself to the simple description of the observed forms, without raising the question of the place which the organism here characterized occupies in the series of known beings,—in what genus, what natural family it is to be arranged; nay, above all, in which *kingdom of nature* it is to be enrolled as a citizen. The settlement of these questions is requisite before anything else, in order to arrive at an actual comprehension of the parts just described.

It is soon seen that it is easier to establish the nearest relationship, particularly the natural family, than to decide the question whether we have to do with an animal or a plant. It is evident at once, namely, *that the organism we have described belongs to the family of the Volvocineæ*. For not only do we find in it the two principal characters which are characteristic of this interesting family; the presence of a number of green globes, which, enclosed in a common colourless envelope, represent a family of cells (polypidom), together with the constant rolling motion which the *Volvocineæ* possess through almost the whole of their life,—but our form also displays, as we shall see hereafter, the third character of the *Volvocineæ*, that the separate globes propagate within the envelope. In fact, there exist the greatest analogies between the known genera of *Volvocineæ*, especially

* Ueber die Verjungung in der Natur, p. 227.

† According to my observations, an alternation of the direction of rotation occurs in *Chlamydococcus pluvialis* similar to that which I have described above (vide Nachträge, &c. l. c. p. 736).

Gonium and *Pandorina*, and the organism here described; and these genera are only essentially distinguished by the arrangement of the green globes or primordial-cells, which in *Pandorina* are placed on a spherical surface, in *Gonium* on a flat plane, while in our form they stand at the circumference of a circle. Since, however, this very law of arrangement is, in the family of the Volvocineæ, the most important criterion, on which the establishment of the genera depends, it follows, that we here have a peculiar genus, which I do not find described either in Ehrenberg's great work or in any later publication.

I owe to the friendly information of Major von Flotow the only notice which can perhaps refer to our form.

In the Berlin 'Haude-Spener's Zeitung' of the 28th of April 1846, namely, occurs the abstract of a paper read by Ehrenberg on April 24th before the Society of "Naturforsch. Freunde." This states that "in this spring he had observed a new generic form of the naked animalcules of the Berlin district, which was closely allied to the green plate-animalcule composed of sixteen corpuscles, called *Gonium pectorale*. Herr Werneck had already discovered an allied new form near Salzburg, which was not tabular but spherical, and formed of eight animalcules, and this he called *Stephanoma*. The new form consisted of 6-21 annularly connected animalcules, was tabular, and each of the corpuscles appeared to bear two proboscides or locomotive organs, with which it moved actively like a rolling wheel. It was denominated *Trochogonium Rotula*."

So far as can be made out from this, unfortunately very imperfect and obscure statement, regarding which I could nowhere find any more minute details, the two genera, *Trochogonium*, Ehr., and *Stephanoma*, Werneck, are the only ones which admit of being placed in a parallel with our form. At the same time, Ehrenberg's *Trochogonium* cannot possibly be identical with the latter, since this is said to be composed of 6-21 globes, while the structure described here is never formed of more than eight green primordial-cells: moreover Ehrenberg says nothing of a spherical envelope; from the statement that its form is tabular and nearest allied to the genus *Gonium*, it seems rather to follow, that a flat envelope exists in *Trochogonium*.

On the other hand, a greater agreement is exhibited by Werneck's genus *Stephanoma*, which Ehrenberg himself mentions as a form generically different from his; and I should not hesitate to call my organism identical with Werneck's, if reasonable doubt were not excited by the expression of Ehrenberg, that the latter is composed of eight, not tabularly, but spherically combined animalcules. For in the above description no distinction is made between the shape of the envelope and the figure formed

by the grouping of the primordial-cells. If, as the meaning of the words indicates, the eight separate cells of Werneck's *Stephanoma* composed a sphere, *Stephanoma* would agree with *Botryocystis Volvox*, inasmuch as the latter genus, furnished with an untenable diagnosis by Kützing, has been applied by Al. Braun to an actually existing being composed of eight (rarely four or sixteen) segments of a sphere surrounded by an envelope pretty closely investing them (Ueber Verjüngung, &c., 170*).

Considering the impossibility of clearing up the relation of *Trochogonium* and *Stephanoma* to our form, from the materials to which I have access, it seemed to me requisite for the interests of science to regard the latter, for the time at least, as a peculiar new genus, and to apply a special name to it. I propose for this *Stephanosphæra* (wreath-globe), to combine in one word the characteristics of the genus, the wreath of primordial-cells and the spherical form of the envelope. Since, moreover, our form has been found in the two stations at present known, in the same way, in rain-water accumulated in hollows of stones, with *Chlamydococcus phuvialis*, and, concluding from the rarity of its occurrence, localities of this kind seem to be characteristic generally for the species, I shall assign to it the specific name of *Stephanosphæra phuvialis*.

IV. On the Systematic Position of the Volvocineæ in general.

The decision of the question whether *Stephanosphæra phuvialis* is to be placed in the animal or the vegetable kingdom is more difficult than the determination of the natural family to which it belongs. It coincides with the general discussion whether the Volvocineæ as a whole are to be regarded as plants or animals. The solution of this question is not only of great importance in a general point of view, but on it is essentially dependent the manner in which we have to interpret the conditions of organization observed in *Stephanosphæra*.

The earliest observer of the genera belonging to the Volvocineæ did not hesitate to regard the persistence and variety of their movements, which never seemed interrupted by an act of germination, as a proof of their animal nature. O. F. Müller already detected in *Gonium pectorale* almost all the details which investigation has reached since (Kleine Schriften, 1782, 15), especially that the entire organism is composed of a great number of separate animalcules held together by a common shield.

* In most works *Botryocystis Morum* is spoken of as a young form of *Pandorina*, and it was figured as such by Ehrenberg; but I have not been able to demonstrate any genetic connexion in the developmental history of the two genera.

Finally, after Ehrenberg had, by his researches on *Volvox globator*, solved the problem in the remarkable structure of that beautiful form, and declared it also, in correspondence with the structure of *Gonium*, a colony of numerous distinct monad-like animalcules combined into a polypidom, he furnished, by a series of important observations on the other genera of *Volvocineæ*, a revision of this family which marked an epoch in the knowledge of it, and even now, in spite of the varying opinions as to their anatomy and systematic character, must be esteemed as the profoundest and most perfect description of this group (Infusionsthierchen, 49-53). His researches went to place beyond doubt the animal nature of the *Volvocineæ*, which, indeed, had scarcely been questioned by any one up to that time. In agreement with his general view of the Infusorial structure, the *Volvocineæ* were regarded as Infusorial Animalcules,—with rigid bodies, with a mouth and many stomachs, but without intestinal canal, with a nervous system and eyes, with testes, spermatie vesicle and green ovules, and lastly, with one or two proboscides, which in many were enclosed in a common envelope or mantle. This mantle was supposed always, except in *Chlamydomonas*, *Syn-crypta* and *Gyges*, to be open in front, so that the animalcules could protrude themselves some distance out and subsequently remove entirely, somewhat in the same way as the Rotifers *Melicerata* or *Tubicolaria*, from their sheaths. The single animalcules were said to propagate independently and develop into new polypidoms inside this mantle (*l. c.* p. 50).

This idea of the structure of the *Volvocineæ* has been almost universally accepted since the appearance of Ehrenberg's great work; and even those naturalists who, like Dujardin, offered opposition to Ehrenberg's doctrine, confined themselves to denying the existence of stomachs and sexual organs to the *Volvocineæ*, without in other respects doubting their animal nature (Hist. des Zoophytes, 307).

In the year 1844 Von Siebold was first led, by a comparison of the moving spores of Algæ with the true Infusoria, to the important declaration, that besides *Closterium* and the *Bacillariæ*, very many of the *Volvocineæ* must be removed from the animal kingdom and placed among plants, since they are destitute of the principal character of animals, contractility. "*Familia infusoriorum Volvocina . . . plene sunt plantis inferiorum ordinum*" (De finibus inter regnum vegetabile et animalia constituendis, p. 12). This view was established* more in detail by Von Siebold in 1848 in his 'Lehrbuch der vergleichenden Anatomie' (p. 7), and

* A form related to the *Volvocineæ*, the genus *Gonium*, had already been described by Turpin as an Alga, under the name of *Pectoralina hebraica* (Mém. de Musée d'Hist. nat. xvi. 1828).

in 1849 in his essay "Ueber einzellige Pflanzen und Thiere" (Siebold and Kölliker's Journal, vol. i. p. 270; Ann. des Sc. Nat. Ser. 3. vol. xii. p. 138; Botanique, 1849).

At the same time scarcely a single botanist has hitherto ventured to claim as lawful property the family referred to the vegetable kingdom through Von Siebold's researches, which zoologists are just as little inclined to give up; and thus even in the last complete enumeration of the Algæ, Kützing's 'Species Algarum' has included only one single genus belonging to the *Volvocineæ*, *Botryocystis*, and this only in consequence of imperfect observation. Only a short time ago a most careful and successful observer, to whom the study of the moving spores of the Algæ owes its first establishment and recently its very complete elaboration, G. Thuret, has seen cause to conclude that the *Volvocineæ*, as well as the *Euglenæ* and even *Tetraspora*, are to be regarded as animals, since they are destitute of the principal character of all vegetable spores, germination (Ann. des Sc. Nat. 1850, Ser. 3. xiv. 214, 61; Recherches sur les Zoospores des Algues et les Anthéridies des Cryptogames).

Only in the last few years has a revulsion appeared to be preparing in this particular, since the study of the *Unicellular Plants* has acquired a greater extension and profundity; and it is in particular the merit of Nägeli to have investigated this hitherto neglected group with a criticism and a completeness of which very few other families can boast (vide his 'Neuere Algensysteme,' 1847, and 'Gattungen einzelligen Algen,' 1849). In consequence of his researches, Nägeli has ventured to include at least two of the forms belonging to the *Volvocineæ*, the genera *Gonium* and *Botryocystis*, among the Algæ.

Lastly, in the past year, the remarkable work of Alex. Braun, 'Ueber die Verjüngung im Pflanzenreiche,' which contains a fund of the most beautiful observations explanatory of the forms standing on the limits between animals and plants, has also fully recognized the notions first set up by Von Siebold on this point, and included the whole family of the *Volvocineæ* in the vegetable kingdom.

I also have been led, by a series of comparative researches, to the conviction, that the assignment of the character of an animal, even only of the lowest *Infusorium*, depends merely on a one-sided criticism of the conditions of organization; that, on the contrary, all analogy of structure and development, as well as the natural relationship, directly indicate to us, that the *Volvocineæ* are to be placed among plants, and indeed in the class of Algæ, in these again in the order of the *Palmellaceæ*, among which they form a special family.

From the contradiction which this assertion has hitherto

almost everywhere met, and since no special establishment of it has ever been given, it appears to me useful to examine the new genus *Stephanosphæra* more minutely from the point of view, by which the relationship of this as well as of the other *Volvocineæ* to plants will be made clear. I have also been led to consider it advisable to give the description of this new Alga in a Journal of Scientific Zoology, because zoologists alone have hitherto taken an interest in the forms of the *Volvocineæ*, and at present appear unwilling to give up to the botanist this interesting family, to which, however, as will be explained in the sequel, they have no valid claim. I may remark, however, that I shall confine myself here solely to *Stephanosphæra*, and reserve for another occasion the examination of the other genera, on which I have collected some new material.

V. Relation of the Volvocineæ to Chlamydococcus.

The most incontestable proof of the vegetable nature of all the *Volvocineæ* is furnished by their relationship to the genera *Chlamydomonas* and *Chlamydococcus*, the developmental history of which has been followed out in its most minute details during the last few years in the researches of Von Flotow, Alex. Braun and myself. The latter genus particularly, which, mingled with *Stephanosphæra*, imparts a red colour to cavities in stones filled with rain-water, has, as the most minutely investigated, furnished the most information not only regarding the general position of the *Volvocineæ*, but also as to the import of the individual portions of their organization.

Dujardin indeed thought that the genus *Chlamydomonas* and the closely allied *Chlamydococcus* ought to be separated from the remainder of the *Volvocineæ*, and that they should be embodied in his *Thecamonadiæ*, nearly the same as Ehrenberg's *Cryptomonadina*; but a more profound investigation, not only of the structure but also of the history of development, teaches us that *Chlamydomonas* (*Diselmis*, Duj.) possesses only external analogies with *Trachelomonas*, while this form, as Ehrenberg already discovered, exhibits the closest alliance to *Gonium* and *Pandorina*. The relation of the colourless envelope to the enclosed green globes, the position of the *two* cilia, which arise from the latter and pass out through the former*, and lastly the laws of division of the green cells inside the envelope, in powers of two, display themselves in exactly the same way in *Chlamydococcus* as in the rest of the *Volvocineæ*; and the only distinction between

* I have already mentioned this condition of the cilia in *Stephanosphæra*; it was detected by Focke in *Pandorina*, and was observed previously by Ehrenberg both in this and *Volvox*.

them consists in the circumstance that in *Chlamydomonas* (and *Chlamydococcus*) the individuals produced by the division of the green globes separate after the absorption of the parent-envelope, and live on as individuals, while in the other *Volvocineæ* the daughter-cells produced by the division of *one* green primordial-cell remain connected by the persistent parent-cell as by a common envelope, and move about as a well-defined body composed of many cells.

While *Chlamydococcus* is a *unicellular Alga in the strictest sense of the word*, never composed of more than *one* cell at any period of its growth, and each division forms the commencement of a new individual, the remainder of the *Volvocineæ* present themselves as *families of cells*, in which a definite number of equivalent cells are combined in some measure into an individual of a higher order. Consequently, *Chlamydococcus* bears the same relation to the rest of the *Volvocineæ* as *Pleurococcus* to *Palmella*, *Cyclotella* to *Meloseira*, or as *Vorticella* to *Epistylis*, and *Hydra* to *Campanularia* or *Tubularia*. On the other hand, *Trachelomonas* and the analogous forms do not belong to the vegetable kingdom at all, but are nearest allied to the *Astasiaæ*, and appear as loricated *Euglenæ* (not as loricated Monads, as Ehrenberg assumed).

The researches of Alex. Braun, like my own, have proved most distinctly that *Chlamydococcus* can only be placed with propriety among the Algæ. It is distinguished, indeed, from the moving germ-cells by which far the greater part of the species of Algæ are propagated, both by a somewhat more complex structure and by the circumstance that the motion lasts for a very long time, and finally, by the power of the moving cells to propagate as such, without entering into the state of rest (germination), otherwise than as quite a temporary condition. But these objections touch only to some extent the specific character of *Chlamydococcus* and the *Volvocineæ* generally as unicellular plants; and they do not stand there among the Algæ altogether without intermediate conditions, as Alex. Braun has proved in his 'Verjungung' (l. c. 227)*, especially from the long movement of the *Volvocineæ*.

On the other hand, the external form, like the chemical and morphological organization of the contents, the laws of motion and the general physiological phenomena, especially however the behaviour in the transition into the condition of rest, in *Chlamydococcus*, agree so perfectly with the moving spores, the transformation of which into undoubted plants has been demonstrated with scientific clearness, that no unprejudiced observer

* Thuret found the swarming-cells of *Ulothrix mucosa* in motion after three days (Ann. des Sc. Nat. 1850, 248).

can discover an essential distinction. I have mentioned in my essay, that Ehrenberg himself, although he claims the moving condition of the forms allied to *Chlamydococcus* as *Infusoria*, has declared the resting-stage of this or a most closely allied genus to be an *undoubted Alga*; and yet the moving Infusoria are only a propagative form of the motionless Alga. Finally, I have succeeded in *demonstrating* the membrane of the cells of *Chlamydococcus* both in the resting, and particularly in the moving stage, to consist of cellulose, and thus of establishing the most important criterion of a vegetable cell we are at present acquainted with, the ternary composition of the cell-membrane, in the Infusorioid condition of *Chlamydococcus*. In fact, all the more recent close observers of *Chlamydococcus*, the number of whom is not inconsiderable, have almost without exception agreed in recognizing, in all conditions of the development of this form, only a plant and nothing but a plant.

Although I refer to the essay above cited in regard to the special physiological and developmental characters of *Chlamydococcus pluvialis*, I cannot omit to include here a sketch of its general course of development, because the key to the comprehension of the *Volvocineæ* generally, and the *Stephanosphæra* here described in particular, lies in that remarkable organism, and in it is revealed most clearly the complete conception of their vegetable nature.

The moving cell of *Chlamydococcus* is composed of two principal parts, a hyaline spherical *envelope*, which is formed of a delicate structureless membrane consisting of cellulose, and immediately surrounds colourless contents, perhaps consisting of pure water. In the centre of the envelope occurs a *coloured globule*, composed of the universal nitrogenous *protoplasm* or *mucus* of vegetable cells, coloured red or green by chlorophyll or a carmine-red oil, and containing imbedded in it numerous *granules of protoplasm*, as well as one or more large chlorophyll vesicles. This coloured globule is attenuated at the upper end into a colourless point; from this go out two cilia, which protrude into the water through two orifices in the membrane of the envelope and produce the movements of the whole. The inner coloured globule is not bounded by any rigid membrane, but merely by a thickened layer of protoplasm; hence its contour is very changeable and passes through manifold transformations in the course of its development. In particular it frequently becomes elongated in all directions into colourless radiating filaments, which keep the internal coloured globule suspended freely in the envelope, and are afterwards retracted in the course of the development (vide my Nachträge, &c. t. 67. A. figs. 27, 28).

The motionless cells of *Chlamydococcus* are of much simpler

structure, and, like all forms of *Protococcus*, consist simply of a tough spherical cellulose membrane and green or red contents organized as primordial utricle. The history of development shows that under certain conditions the contents of the motionless cells become divided into a number of portions, which always correspond to two, or a power of two in their number; that these portions become organized into special primordial utricles, and as such break through the parent-cell, each developing two cilia, and by the aid of these rotating actively in the water. During their motion they excrete a delicate cellular membrane over their entire surface, which is gradually removed farther and farther from the primordial utricle by endosmose of water, until at length it becomes the wide envelope of the moving form described above (Nachträge, tab. 67. A. figs. 23, 35, 29). From this it follows that the latter forms do indeed possess on the whole the character of simple cells, but display some peculiarities in their structure and development, since the internal coloured globule corresponds originally to the primordial utricle of other vegetable cells, yet is not surrounded by a membrane, as usual, but suspended free in it like a cell-nucleus, while watery, unazotized contents appear between the membrane and the primordial utricle. For this reason I have called the enclosed coloured globule, which is formed first, and originally moves about without a special membrane in the manner of a cell, and corresponds to the primordial utricle of vegetable cells in general, the *primordial-cell*, and the enclosing membrane with its watery contents the *envelope-cell*. The moving *Chlamydococcus*-condition is capable of propagating as such, by the enclosed primordial-cell dividing anew, the individual portions slipping out of their envelope-cell and running through the cycle of development of their parent-cells. In passing into the state of rest, the enclosed primordial-cell secretes over its surface, inside its envelope, like every primordial utricle, a new tough cellulose membrane, and through this metamorphosis assumes the form of an ordinary *Protococcus-cell*, while the envelope-cell is dissolved (Nachträge, tab. 67. B. figs. 91, 92, 93). But only such primordial-cells behave in this way as are produced by the division of a *Chlamydococcus*-globule in a lower power of two; the primordial-cells originating from a 16-64-fold division move far more actively and do not secrete an envelope-cell; they are incapable of any propagation and pass immediately into the condition of rest (*l. c.* tab. 67. A. figs. 56-62, tab. 67. B. figs. 79, 80). Alex. Braun has called these forms of *Chlamydococcus*, which develop an envelope-cell, *macrogonidia*, and distinguished the smaller ones originating from multifold division, as *microgonidia*.

VI. *Comparison of Stephanosphæra with Chlamydococcus.*

If we now compare the conditions of organization of *Stephanosphæra* with those of *Chlamydococcus* which we have just indicated, we find the most essential agreement. In the first place the envelope-cell of *Stephanosphæra* corresponds exactly to that of the moving macrogonidia of *Chlamydococcus*; it is composed of a delicate colourless membrane and contents resembling water. Chemical actions to which I subjected the envelope-cell of *Stephanosphæra*, bear witness of this agreement in the most minute particulars. The envelope-cell is indifferent to acids and alkalies and is not dissolved in them; but it suffers a peculiar thickening by sulphuric acid which causes it to apply itself more closely to the primordial-cell, and present itself very distinctly and clearly defined. In general the application of *dilute sulphuric acid* is often the best means of making clear delicate vegetable membranes which would otherwise be readily overlooked, especially when iodine is added, which then ordinarily colours the membrane yellow. The cilia also are rendered more distinct by sulphuric acid. The envelope-cells of *Pandorina*, *Chlamydococcus* and *Volvox* behave in exactly the same way.

With regard to the chemical composition of the envelope-cell of *Stephanosphæra*, I have succeeded in demonstrating in it also the most decisive criterion of a vegetable membrane. Since Nägeli, in his comparison of the Unicellular Algæ with the simple animal cells, arrived at the result, that all distinctions hitherto proposed between the lowest forms of the two kingdoms are fallacious, and that the only decisive criterion must lie in the nature of the membrane, which belonged in animals to the proteine series, and in plants to the group of hydrates of carbon—since that epoch attention has necessarily been directed, in all amphibolic structures, to the investigation of the chemical composition of their membrane. I have *succeeded in demonstrating the characteristic reaction of vegetable cellulose, the blue colouring by iodine and sulphuric acid, in the envelope-cell of Stephanosphæra.* For this purpose it is requisite to allow a drop of *pretty concentrated sulphuric acid* to act upon the swarming *Stephanosphæra*-globes until the green primordial-cells in the interior are decomposed, by which time the proper transformation of the envelope-membrane has taken place, and a drop of solution of iodine (iodine in iodide of potassium), sufficiently diluted to prevent the sulphuric acid precipitating it in crystals, then produces a coloration of the envelope, which appears *at first violet, gradually becoming more intense, and at last beautiful indigo blue.* Thus the chemical behaviour of the envelope-cell in *Stephanosphæra*, as

in *Chlamydococcus*, is the most evident proof that the organisms to which they belong cannot be regarded as Infusoria, but are simply Algæ. Moreover this behaviour of the envelope-cell of *Stephanosphæra* shows that the latter is bounded by a true cellulose membrane, and not, as is assumed almost universally of the *Volvocineæ*, and by Nägeli even of all Algæ, of secreted mucus or jelly*. The direct observation of the envelope-cell of *Stephanosphæra* likewise shows that this is completely closed in its normal condition, and only perforated by orifices in the spots where the cilia of each primordial-cell pass out. Not until a later stage, when the primordial-cells singly leave the envelope or have begun to propagate, does the membrane of the envelope tear, gradually collapse and become dissolved, so that the included globes can make their exit freely.

It is obvious that the eight green globes of *Stephanosphæra* correspond exactly to the primordial-cell of *Chlamydococcus*. The primordial-cells of *Stephanosphæra* consist in like manner of nitrogenous protoplasm, in itself colourless, which is coloured brown by iodine and almost wholly dissolved by caustic potash and ammonia. The protoplasm is coloured by the universal colouring matter of vegetables, *chlorophyll*; for alcohol and æther bleach the green globules, and concentrated sulphuric acid changes the green colour into a verdigris-green or blue—a reaction which, from my observations, is characteristic of chlorophyll (vide my essay on *Loxodes Bursaria*, Siebold and Kölliker's Journal, iii. 264).

The chemical nature of the fine granules in the primordial-cells which with age multiply, so that the primordial-cells at length lose their transparent green colour and appear dull, opaque and olive-brown, is difficult to determine on account of their small size; they are either *protoplasm-granules*, or, as a bluish colour given by iodine might lead one to conclude, perhaps *starch-granules*. On the other hand, the *two darker nuclei* in each primordial-cell are undoubtedly the same structures which occur in *Chlamydococcus*, and in like manner not only in all the *Volvocineæ*, but also in most of the Algæ of the orders of *Palmelleæ*, *Desmidiæ*, *Confervæ*, &c. Nägeli has called these *chlorophyll-utricles*, and demonstrated their universal occurrence in the vegetable kingdom by comparative descriptions (Gattungen einzelliger Algen, ii.). Ordinarily there exist only *two* in *Stephanosphæra*, which may be distinguished in the earliest stages, while among other *Volvocineæ*, for instance, *Gonium* contains only *one chlorophyll-utricle*. It is difficult to settle anything definite

* The common envelope of *Gonium* is certainly composed of a gelatinous substance without a bounding cellulose membrane.

concerning their structure and function; they must not be regarded as cell-nuclei, although they resemble them very much, especially when only one is present. Caustic potash, which destroys the rest of the contents of the primordial-cells, makes the chlorophyll-utricles of *Stephanosphaera* show themselves more distinctly as hollow rings, surrounded by a membrane which is rather granular; iodine colours them *deep violet*, which leads to the conclusion of the presence of starch*. Ehrenberg thought the chlorophyll-utricles were to be recognized as the testes of the *Volvocineæ*; it is certain, however, that these structures may be seen in greater or less number, in exactly the same way, in undeniable plants, such as *Hydrodictyon*, *Cedogonium*, *Mougeotia* and others (vide, among others, H. von Mohl's Treatise on the Vegetable Cell, in R. Wagner's Handwörterbuch der Physiol. pl. 1. figs. 20-24, and in the English Translation ditto).

I have already shown that the primordial-cells of *Stephanosphaera* as well as those of *Chlamydococcus* are destitute of a special rigid membrane; consequently they do not correspond to perfect cells, but on the whole only to primordial-utricles. In like manner the curious colourless mucous filaments which extend out from the extremities of the primordial-cell of *Stephanosphaera*, are evidently analogous to the rays which make one condition of the *Chlamydococcus*-cells look hairy (var. *setiger*, V. Flotow). They are merely prolongations of the colourless protoplasm forming the substance of the primordial-cells, and correspond pretty well morphologically to the reticulated branching filaments of protoplasm, the sap-currents as they are termed, which maintain the nucleus suspended freely in the interior of the cells of the articulations of *Spirogyra*, or of the hairs of the anthers of *Tradescantia*. Alcohol and acids cause these prolongations to be retracted into the substance of the primordial-cells; the same thing takes place during the course of the development. Ehrenberg has called these peculiar mucous rays, which also occur in some other *Volvocineæ*, in some cases a *tail* (*Synura*, *Uroglæna*), in others connecting canals or indications of a vascular system (in *Volvox* and *Gonium*). These protoplasm-filaments naturally present a different aspect according to the shape and arrangement of the primordial-cells: while they appear as a wreath of cilia in the globular *Chlamydococcus*-cell, in the more spindle-shaped *Stephanosphaera* they rather resemble

* It is well known that the chlorophyll-utricles of most of the Algæ, as well as the analogous chlorophyll-globules occurring in the cells of almost all Phanerogamia, secrete starch. Alex. Braun indeed has called the corresponding structures in *Chlamydococcus pluvialis* simply "Amylon-globules," in which may be detected an envelope and a nucleus (Verjungung, 222).

bundles of rays passing out from each end; in *Volvox*, if seen only from above, they give the individual primordial-cells a polygonal, radiating aspect, and form threads of communication between them: Focke has wrongly considered them as intercellular passages between the individual animalcules. The connecting threads in *Gonium*, on the other hand, are something quite different, and do not belong at all to the domain of the protoplasm-filaments, as I shall explain more fully at another opportunity.

Thus the microscopic analysis, like the chemical investigation of *Stephanosphæra*, in exact analogy with *Chlamydococcus* and the swarming-cells of the other Algæ, has enabled us to distinguish all the characters of a plant, but not one mark of a true animal organization, in particular not a trace of a mouth, stomach, and sexual organs. But the genus *Stephanosphæra* is thereby pre-eminently important for the decision of the question of the limit between the animal and vegetable kingdom, *because the history of its development affords the most convincing proof of the vegetable nature of this genus, and thus of all the other Volvocineæ.*

VII. Development of *Stephanosphæra*.

Both the very delicate envelope-cell and the widely distant, transparent green globular primordial-cells of the young *Stephanosphæra* are of a relatively small size. Both grow so much as to double their dimensions during their vegetation; the former acquires a tough membrane; the latter fill up the greater part of the envelope-cell, advance towards each other so as to touch, develop thicker, denser contents, and assume most curious forms through the ramification of the protoplasm-filaments. Finally the process of propagation shows itself in the primordial-cells. The radiating ends retract all their prolongations, and become rounded into a perfect sphere; the primordial-cells are now merely attached to the envelope-cell by their cilia, and thus are readily moved from their normal corresponding positions, and then appear devoid of any definite arrangement in the envelope-cell (fig. 8).

These changes take place in the course of the afternoon; towards evening more influential metamorphoses make their appearance. The primordial-cell, namely, extends itself predominantly in *one* direction in the axis perpendicular to the equatorial plane, consequently in the position which fig. 2 represents from above downwards. The two chlorophyll-utricles respectively repair to the two ends; the green contents likewise flow chiefly to the two sides, and leave a broad colourless zone visible in the middle, such as we observe somewhat in the same position in

Closterium (fig. 8). Finally the primordial-cell becomes constricted, gradually from the periphery to the centre, in the middle line, and is thus divided into two secondary cells, the septum of which, in the position above assumed, runs from right to left (in the diagrammatic figure 21 from *a* through *m* to *b* and *n*). Each of the halves cut off by the division then expands somewhat in the direction from left to right; a new constriction soon presents itself in the direction from above downwards (in the diagram fig. 21 from *c* through *m* to *d* and *n*); when this is complete, the originally globular primordial-cell is divided into four quarters (figs. 8, 9).

This process of constriction and cutting off is repeated *once more*, each secondary cell becoming divided by a new septum into two equal halves (fig. 10). The division takes place through two of the largest circumferences, passing from before backwards, and cutting the points *m* and *n* through which the two preceding septa passed: on the diagram fig. 21 these are represented by the circles *e, f, m, n,* and *g, h, m, n*. Since the originally globular primordial-cell has meanwhile only expanded in the direction of the two axes going from above downwards and from right to left, and is not enlarged in the third direction, from before backwards, the whole presents the form of a flattened spheroid, somewhat of the shape of one of our loaves (the shape of a *turban*, or of the bowls used on the bowling-green), which is divided into eight equal segments, meeting in the middle, by four ellipses distant 45° from each other, and intersecting in the axis of rotation (vide figs. 10, 13 & 21).

This process of division, by which each primordial-cell produces in the first generation two, in the second four, and in the third eight secondary-cells, is completed in the course of the night, so that early in the morning, in the long summer days even by 3 o'clock, we perceive each of the eight primordial-cells divided into eight in the manner described (figs. 10, 11). The generations produced in each case by this triple subdivision vary in the duration of their lives and in their capacity of development; the first two rapidly divide again, and therefore are, according to Nägeli's expression, mere '*transitional generations*'; the third alone arrive at complete development and persist a long time as such; these form the '*permanent generation*.'

The process of division does not always take place simultaneously in all the eight primordial-cells of *Stephanosphaera*; we not unfrequently find inside the same envelope-cell some primordial-cells still wholly unaltered, while others are already preparing to divide into two, a third perhaps already into four, and a fourth has already resolved itself into its eight secondary-cells (vide fig. 8). Very often most of the primordial-cells are found

already completely separated into eight, while one or other of them is still wholly unaltered.

When the act of division has gone on favourably up to the point to which we have followed it above, some hours elapse before the young families of cells escape completely from the envelope. The process which precedes their birth consists principally in the more complete isolation, in a centrifugal direction around their common centre, of the secondary-cells produced by *each* primordial-cell. Since the parting off of the secondary-cells advances gradually from the periphery towards the centre, they are already completely individualized and separated by intercellular spaces at the periphery, while all eight remain still connected in the centre into a common colourless mucous mass filled with protoplasm-granules (fig. 11). But the flow of the contents from the centre to the borders, which continues up to this time, at length causes the constriction of the central mass of protoplasm also into eight parts; the eight secondary-cells then appear of a deep yellowish green externally, passing internally into colourless green towards finely granular beaks which are all connected in the centre, but become gradually attenuated, torn away and retracted (figs. 10, 11, 13, 14). Then the young primordial-cells become rounded into short cylinders and stand in a circle, without organic connexion, but placed closely beside one another: seen from above (in the polar view), under the microscope, they resemble a wheel with eight notches; from the side, examined in the equatorial view, we see four or eight short cylinders lying side by side, so that the whole is not unlike a small *Scenedesmus obtusus* (fig. 11 a).

The primordial-cell undergoing division behaves as a *whole* towards external things, until the parting off into eight is quite completed; that is to say, its two cilia move uninterruptedly, and consequently the entire *Stephanosphaera*-globe still rolls through the water according to the known laws, even when most of its primordial-cells have already become more or less completely divided into four or eight secondary-cells. Only shortly before the completion of the division do the cilia of the *parent-cell* lose their motion and disappear, it may be by being retracted or by being thrown off; but the orifices through which the cilia previously passed out into the water, may now be observed in the common envelope-cell, as minute points surrounded by a thickened border.

Immediately after that, it is seen that the newly-formed secondary-cells have developed their own cilia; for the young generations formed in the interior of the parent-envelope now begin to move and to roll over like a wheel, so far as the confined space allows of this (figs. 11, 12). In consequence of this

movement of the eight small wheels rotating in the interior of the common envelope-cell, which constitutes a very pretty object, the parent-cell soon becomes enlarged and attenuated at certain points; the cellulose of which it is composed appears to be transformed into soluble jelly, and soon afterwards one after the other breaks through out of the common envelope and revolves freely and independently in the water, according to the same laws as the old spheres, but more actively and energetically. The young *Stephanosphæra* exactly resembles a green wreath composed of eight small cylinders, upon which by itself no envelope and cilia can be detected (fig. 13); but if killed with iodine, the eight primordial-cells are seen to be surrounded by a common envelope-cell in the form of an exceeding delicate membrane; only this lies in all parts almost immediately upon the green globes, so that it follows the waved outline they produce, and in its total form resembles a flat spheroid with eight notches on its border; it is perforated by the cilia, which go off in pairs from each of the primordial-cells; and two chlorophyll-utricles are already distinguishable in the latter (fig. 14). By degrees the envelope-cell is lifted up by the endosmotic absorption of water; its surface becomes smoothed out, and it appears circular in the polar view; on the other hand, it retains for a longer time the form of an almost tabular spheroid, and hence presents an ellipse in the equatorial view (fig. 15); finally it expands uniformly in all directions and thus acquires its normal spherical form, while at the same time it becomes considerably thickened. This whole process of propagation is completed during the night, and on bright days *Stephanosphæra* are rarely seen in course of division at sunrise; on dull days they may be observed in this condition in the first part of the morning.

The primordial-cells, however, not unfrequently come to a standstill in the stage of division of the second generation, so that they only separate into four secondary-cells; these at once develop cilia and an envelope-cell, without dividing a third time, and make their exit from the parent-envelope in this condition. Here therefore only the *first* generation of each primordial-cell is a *transitional generation*, the *second* already a *permanent generation*. Hence arises the circumstance that we often find among other eightfold *Stephanosphæra*-globes, some in which the envelope-cell encloses only four primordial-cells standing at equal distances, which in other respects behave in the ordinary manner (fig. 7).

It is still more frequently observed, when the primordial-cells have already become constricted into four secondary cells and are beginning to divide again into eight, that this process of division is not perfectly completed in all four portions, but that

the young *Stephanosphæra* already becomes free and develops the envelope-cell, *although one or other of the four quadratic segments of the sphere has become constricted but not parted off*. Hence originate monstrous forms, since the general envelope-cell then encloses only seven primordial-cells; but in these cases it is always observed that one of them is distinguished by most curious prolongations or mucous filaments, that it appears twice as large as the rest, that it contains four chlorophyll-utricles instead of two as is usual, and that it is also more or less constricted in the middle. All this furnishes proof, that here *one* secondary-cell of the second generation has not been divided the third time like the rest, but occupies by itself the space which is ordinarily filled by two. Very often only six (fig. 6), or even no more than five primordial-cells are found in one envelope-cell; but then two or three of these are twice as large as elsewhere*. In like manner Alex. Braun figures a *Pediastrum* composed of fifteen instead of sixteen cells, wherein one however is twice as large as the rest (Verjungung, t. ii. 20).

On the whole, it is obvious that the mode of propagation of *Stephanosphæra* already examined corresponds completely to that we are already acquainted with as *formation of macrogonidia* in *Chlamydococcus*. In both cases it depends upon the envelope-cell remaining unaltered, while the primordial-cells become divided, first into two secondary cells, and then so on in a lower power of two, each of the secondary-cells immediately developing two cilia, and secreting over its whole surface, as do all primordial-utricles of vegetable cells, a delicate cellulose membrane, which however becomes gradually removed further from the secreting primordial-cell through absorption of water. The only distinction between *Chlamydococcus* and *Stephanosphæra* arises from the formation of a special envelope-cell to each individual secondary-cell in *Chlamydococcus*, while in *Stephanosphæra* all the generations produced by division form *one* primordial-cell, become enclosed by a common envelope, and move away as *families of cells*. On the contrary, the developmental history of

* Only such imperfect division of a transitional generation gives the possibility of the green cells occurring otherwise than in a power of two, in *Stephanosphæra*, as in all the other *Volvocineæ*, in which the same law holds good; at most the normal number might be rendered imperfect by the emission of one or other of the cells which occurs sometimes. On the other hand, definitions like that of Kützing's *Botryocystis Morum*, which is pretended to be composed of six secondary- (primordial-) cells, evidently have their origin merely in imperfect observation and misapprehension of the law of division. In like manner, Ehrenberg's statement that the number of individuals in his *Trochogonium* varies from six to twenty-one, may depend upon a neglect of the proper character. In general, the earlier observers have frequently overlooked the constant numerical relations in the structure of the *Volvocineæ*.

Gonium, *Pandorina* and *Volvox* agrees in all essential particulars with the laws of propagation, which I have just described in *Stephanosphaera*, as will be shown elsewhere. We may call the mode of multiplication of the *Volvocineæ* by the general name of *propagation by macrogonidia*.

Another process is met with in *Stephanosphaera*, besides the above, and which I have observed more rarely, viz. *propagation by microgonidia*. In this mode of multiplication the introductory processes are exactly like those of the formation of macrogonidia; in particular each primordial-cell is at first divided into two, then into four, and lastly into eight secondary-cells. But instead of this third generation being permanent and becoming free, as is usual, it not unfrequently happens that the process of division is not arrested with the separation into eight; that the original primordial-cell becomes parted off a fourth, fifth, and even a sixth time, in the same manner, and *at length is broken up into a large number of cells* (16, 32, 64), which naturally are so much the smaller the greater number of times the subdivision into two has taken place (fig. 16). While, moreover, in the formation of macrogonidia, the secondary cells become surrounded by a common envelope, and are not free as an entire, connected family of cells, arranged according to a definite law, in the mode of propagation now described the *little secondary cells finally become totally separated from one another*, without secreting an envelope-cell, and in this way each of the eight original primordial-cells is broken up into 32-64 independent, green, elliptical or spindle-shaped corpuscles, which then separate from one another, commence an independent and active motion, and fill up, in great numbers (as many as 256-512), the common parent-envelope-cell. These little cellules—I shall follow the example of Alex. Braun and call them *microgonidia*—exhibit a very active and energetic motion inside the envelope-cell, hurrying very rapidly up and down in all directions in its cavity; producing by their great number that curious swarming which Alex. Braun has very aptly compared with the intermingling of a crowd of people in a confined area, where every one is constantly changing his place, while the whole together constantly occupy the same space. This *crowding in among each other* of the microgonidia of *Stephanosphaera* presents a picture fixing the attention in the highest degree; sometimes the cellules are scattered in a few large masses; then they unite again into a knot in the middle; every moment the general aspect varies (figs. 17 & 18). At length the common envelope is ruptured here also; then the microgonidia emerge one after another or in large masses, but free and singly, into the water (fig. 19 a). Their true form may be then readily detected by killing them with iodine; they are *spindle-*

shaped and acuminate at both ends, bright green in the middle, and run out into a colourless beak at each end, on the whole not unlike young *Euglenæ*, without trace of an envelope-cell; the extremity which goes first in their swimming bears delicate cilia; the number of the cilia is four (fig. 19). When the microgonidia reach the water they move most actively in all directions, and in a short time all the corpuscles emitted from an envelope-cell are scattered and disappear in the wide surface of the drop of water.

I have not been able to make out what becomes of the microgonidia subsequently, since they are ordinarily decomposed on the object-holder after a brief swarming; but it may be conjectured that they also serve for propagation, and probably pass into a condition of rest. At least the latter has been observed in the microgonidia of *Chlamydococcus phuvialis* by Alex. Braun and myself: the history of the development of the latter agrees wholly with those of the *Stephanosphæra*; they originate also by the division of the primordial-cell in a higher power, are distinguished by their minute size and more active, peculiarly Infusorioid movement, and never develop an envelope-cell during their movement. The microgonidia of both therefore are true primordial-cells; that is, primordial-utricles resembling cells, organized exclusively of coloured protoplasm, without any cellular membrane*. The only distinction between them is, that the microgonidia of *Chlamydococcus*, like their macrogonidia, possess two cilia, while in those of *Stephanosphæra* I observed four. That the microgonidia of *Stephanosphæra* correspond perfectly in morphological respects to the macrogonidia, and only depend upon a higher power of division, is proved by a case in which seven out of the eight primordial-cells in one envelope-cell were broken up into microgonidia, while one divided merely into eight secondary-cells; the latter were developed as macrogonidia and formed a connected wreath surrounded by an envelope-cell, which rolled slowly about in the parent-envelope, surrounded by the swarm of free, rapidly moving microgonidia (fig. 18 a). Alex. Braun has also observed a formation of microgonidia in *Chlamydomonas obtusa*; probably all the rest of the *Volvocineæ* have a formation of small isolated microgonidia which become free, as well as the ordinary propagation by large macrogonidia arranged in families of cells.

* In these, and generally speaking in most swarming-cells of Algae, we have structures which in their development and independent individualization, their vital processes and their mode of movement, behave exactly as cells, but are composed solely of cell-contents, without cell-membrane; a proof that in the vegetable kingdom even the definition of the cell must be in many cases conceived in a more extended sense than might be assumed from the schemata of our manuals.